

Dental Variation Among Asian Colobines, with Specific Reference to the Macaques on the Same Continent

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Abstract: In order to discern dental morphometric variations among the Asian colobines, residuals of the colobines, derived from allometric baselines formed by the Asian macaques (*Macaca*), were analyzed with Principal Components Analysis and Euclidean Distances. Results indicated that the widely accepted view that the colobines possess relatively smaller front teeth than the macaques is only the case for the first incisors. The colobines show relatively smaller molars than the macaques. Such profiles may be related to the differences in dietary preferences between the two major groups of the Asian Old World monkeys. The magnitude of such differences is not as great as usually assumed for the two groups that contain both African and Asian taxa. In other words, the two Asian cercopithecoid groups may have homogenously been shaped by the tectonic modifications and climate alterations in the past five million years. There exist marked differences among the Asian colobines when each of the genera is compared with macaques; the dental profile reflects not only the variation in geographic distribution but also in phylogenetic divergence. Thus, the snub-nosed monkeys (*Rhinopithecus*) and the gray langurs (*Semnopithecus*) are characterized by relatively larger molars than the other colobines – larger even than those of the macaques. The differences among Asian colobines, depicted by Euclidean Distances, seems to reflect the relationship of the phylogeny and evolution between colobines and cercopithecines.

Key words: Asian colobines; Macaques; Dental; Morphometric variation; Ecological and geographic alternation; Functional adaptation; Phylogeny and evolution

亚洲疣猴与猕猴牙齿的比较

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摘要: 为了研究亚洲疣猴牙齿形态与功能适应性之间的关系, 建立异速生长公式比较分析生活于同一大陆的猕猴。主成份分析用来分析来自异速生长公式的残差。结果表明: 疣猴出乎意料地展示了比猕猴更小的门齿。导致此结果的可能原因是: 疣猴与猕猴之间的食物差异性。但是, 这种差异小于亚-非大陆种类。也就是说, 在过去的 500 万年左右的时间里, 生活于同一大陆的疣猴和猕猴已经产生了一些对环境和食性的趋同性。当每一个疣猴属分别与猕猴进行比较时, 它们之间的差异性揭示了地理分布的差异。金丝猴 (*Rhinopithecus*) 和长尾叶猴 (*Semnopithecus*) 具有比其他疣猴发达的臼齿。欧氏距离的结果说明疣猴和猕猴牙齿的差异性揭示了它们在系统发育方面的关系。

关键词: 亚洲疣猴; 猕猴; 牙齿; 形态变异; 生态和地理; 功能适应; 系统发育与进化

中图分类号: Q959.848 **文献标识码:** A **文章编号:** 0254-5853-(2007)06-0569-011

Asian colobines, like other Old World monkeys on the same continent, display great biodiversity in many aspects (Rowe, 1996; Brandon-Jones, 1998; Fleagle, 1999; Pan, 1998; Kirkpatrick et al, 2001). Some species are now found in the tropical and subtropical forests, swamp forests along coastlines and on islands. Others are confined to the plateaus, such as the Qinghai-Tibet

Plateau next to the Himalayas, where they have adapted to the highest altitudes of any non-human primate. Thus, they have been greatly shaped in their morphology, dietary preference, functional adaptation and behavior (Davies & Oates, 1994).

A recent morphological study on the third molars has revealed considerable variation among the Asian

Received date: 2007-04-30; Accepted date: 2007-09-29

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colobines, in particular the species of *Presbytis* (Willis & Swindler, 2004). Another recent dental morphometric study on the Asian colobines has highlighted the views on their phylogeny and functional adaptation (Pan & Oxnard, 2003), in which four groups were identified (*Rhinopithecus*, *Semnopithecus*, *Trachypithecus* and the *Nasalis*, *Pygathrix* and *Presbytis*), corresponding to the similarities in their dental morphology and dietary preferences. The study, however, focuses only on the Asian colobines, without providing a comparison with other primates (outgroups), the macaques, which are on the same continent and closely associated in terms of phylogeny and evolution (Delson, 1980, 1994; Pan & Jablonski, 1987; Andrews et al, 1996; Fa, 1989; Jablonski et al, 2000). The current study compares colobine dental variation with that of the macaques that are generally sympatrically distributed with colobines on the same continent, though some macaques are distributed further north close to Beijing, China (*M. mulatta*) and far east into Taiwan (*M. cyclopis*) and Japan (*M. fuscata*). These northern and eastern extensions are, however, only recent – Late Pleistocene and Early Holocene (Delson, 1980; Fa, 1989; Pan, 1998; Pan et al, 1992). In other words, colobines and macaques in Asia overlap geographically although they have developed alternative dietary preferences and locomotion patterns (Fooden, 1982; Pan, 1998; Davies & Oates, 1994; Rowe, 1996).

Some evidence suggests that these two groups separated at about the Middle Miocene and have evolved independently since then (Pilbeam & Walker, 1968; Simons, 1969; Shoshani et al, 1996). They have existed, however, through the same set of environmental changes since the Early Pliocene in Asia. Particularly, the two major events that greatly impacted on the biological world of Asia: the rapid uplift of the Qinghai-Tibet Plateau and the last global glaciation, 6,000 years ago (Pan & Jablonski, 1987; Yim & He, 1988). They then radiated throughout most of Asia where they are now sympatrically distributed (Pan & Oxnard, 2001a).

The different dietary habits of the two Asian primate groups are associated with a number of anatomical and physiological differences in their digestive systems. Thus, colobines are characterized by long digestive tracts with specific gastric adaptations for handling leaves. Macaques, in contrast, are distinguished by buccal pouches and a shorter gut, necessary for digesting fruit (Disotell, 1996; Caton, 1998; Ye et al,

1987; Kay & Davies, 1994). There are, in addition, differences between their dentitions; macaques tend to have bigger anterior teeth, which has been hypothesized to relate to the cutting and grasping of fruits; and the colobines, in contrast, are assumed to have developed larger postcanine teeth, especially molars, to adapt to crushing, shearing and grinding of leaf fibers (Hylander, 1975a, b; Kay, 1975). Such variations in morphology relate to their different diets and as a result macaques are generally regarded as frugivorous and colobines as folivorous (Napier & Napier, 1967; Goldstein et al, 1978; Smith, 1983; Smith et al, 1983). These studies, however, involve the taxa from both Africa and Asia, and thus cover greater variation in many aspects, such as climate, vegetation and landscape (Gould, 1975). More recent investigations indicate that such descriptors are ambiguous (Bennett & Davies 1994; Oates et al, 1994; Rowe, 1996). For example, there is great diversity of dietary preferences from season to season within species (e.g. in red colobus, Chapman et al, 2002), and from region to region in some Asian colobines (Oates et al, 1994) and macaques (Zhao et al, 1991; Hanya, et al, 2003; Hanya, 2004).

Thus, the main purpose of this study is to explore dental variation patterns among the Asian colobines, and determine how such variation is principally related to functional adaptation and phylogenetic development, when the macaques on the same continent are used as a contrast group.

1 Material and Methods

The species and sample sizes used in this study are listed in Tab. 1. All of them were from the collection of Asian Old World monkeys and judged as adults by the full development of M3s. The left sides of the maxilla and mandible were used to take maximum dental length (anterior-posterior dimension) and width (buccolingual dimension). Widths of the incisors and canines are buccolingual distances above the alveolar processes. The right side was utilized if the left one was damaged or missing. Measurements were taken from materials in a number of universities, museums and other academic institutions (see Acknowledgments).

Because of the irregular shape of the molars, methods of scaling teeth are quite variable. Some scholars use crown area – maximum length \times maximum width (Gingerich et al, 1982; Kieser & Groeneveld,

Tab. 1 Asian colobines and macaques used in this study*

Species	Common names	Female	Male	Total
Colobines				184
<i>Rhinopithecus roxellana</i>	Golden snub-nosed monkey	8	10	18
<i>R. bieti</i>	Black snub-nosed monkey	9	8	17
<i>R. brelichi</i>	Grey snub-nosed monkey	1	3	4
<i>R. avunculus</i>	Tonkin snub-nosed monkey	2	2	4
<i>Pygathrix nemaeus</i>	Red-shanked douc langur	8	9	17
<i>Nasalis larvatus</i>	Proboscis monkey	3	5	8
<i>Presbytis rubicunda</i>	Maroon leaf monkey	7	5	12
<i>P. comata</i>	Javan leaf monkey	3	4	7
<i>P. melalophos</i>	Banded leaf monkey	5	5	10
<i>Semnopithecus entellus</i>	Grey langur	5	5	10
<i>Trachypithecus vetulus</i>	Purple-faced leaf monkey	5	3	8
<i>T. phayrei</i>	Phayre's leaf monkey	9	8	17
<i>T. francoisi</i>	Francois' leaf monkey	7	8	15
<i>T. obscurus</i>	Dusky leaf monkey	10	10	20
<i>T. cristatus</i>	Silvery leaf monkey	9	8	17
Macaques				304
<i>Macaca mulatta</i>	Rhesus monkey	20	20	40
<i>M. fuscata</i>	Japanese monkey	11	11	22
<i>M. sinica</i>	Torque monkey	8	14	22
<i>M. assamensis</i>	Assamese monkey	20	20	40
<i>M. radiata</i>	Bonnet monkey	12	12	24
<i>M. arctoides</i>	Short-tailed monkey	20	20	40
<i>M. nemestrina</i>	Pig-tailed monkey	20	20	40
<i>M. nigra</i>	Crested black monkey	8	8	16
<i>M. fascicularis</i>	Crab-eating monkey	20	20	40
<i>M. thibetana</i>	Tibetan monkey	8	11	20

* Classification of colobine species is referred to that used by Oates et al (1994).

1990). Others utilize greatest length or width (Gordon, 1982). Yet others apply a specific equation – maximum (mesiodistal) length \times (medial width + distal width)/2 (Freedman, 1957; Delson et al, 2000). In this study crown area is gauged as the maximum length multiplied by maximum width.

Colobines and macaques have a large spectrum in terms of body size (Smith & Junger, 1997; Pan, 1998; Delson et al, 2000) and this is related to dental size (Delson et al, 2000). As a result, the latter is frequently used to predict the body size of fossils (Pilbeam & Gould, 1974; Gould, 1975; Pan & Peng, 1995; Delson et al, 2000). Thus, a certain research method that is able to reduce size-related variation has to be used for the study. This will allow a clearer investigation of functional adaptation and phylogenetic divergence (de Winter, 1997). One of these methods is the analysis of the residuals generated from a common allometric baseline. Variation in the residuals illustrates how much an individual or taxon deviates from a specified allometric formula (baseline) (Smith 1983; Bouvier 1986; Pan & Oxnard, 2001a; Pan et al, 2002).

Statistically, the scales of the dependent and the independent variables in the allometric analysis must be the same (millimeters in this study) in order to maintain geometrical and mathematical unity. Thus, the square root (SR) of a dental crown area (mm²) is calculated before being used as the dependent variable in the usual allometric formula: $Y = aX^b$ or $\log Y = \log a + b \log X$; where, Y is the dependent variable, SR of the tooth, and X is the independent variable, body size.

Body size (weight) is the variable (component) against which other body variables, such as physical movements, behavioral preferences, dietary selections, physiological responses and metabolic processes can be compared (Jungers, 1985; Jungers et al, 1998). In most cases, however, records of the body size are not available, so other measurements, such as, cranial length and width (Pilbeam & Gould, 1974; Gould, 1975; Pirie, 1978; Wood, 1979; Eaglen, 1984; Delson, et al, 2000; Pan & Oxnard, 2001a; Willis & Swindler, 2004), dental size and postcranial measurements – lengths and mid-shaft diameters of the humerus (Delson, et al, 2000), have been used as a surrogate for body size. A recent study

aimed at exploring the relationships between body size and craniodental dimensions and postcranial measurements, respectively for the cercopithecoids indicates that particular cranial dimensions, such as neurocranial length, show a high correlation with body size (Delson et al, 2000). In this study, cranial length – the distance from the glabella to the tip of the occipital protuberance (surrogate for body size) – was the independent variable.

Ten species of the Asian macaques (*Macaca*) were used to set up an allometric formulae, based on which the residuals for the colobines were produced through the following formula: $RD \text{ (residuals)} = \text{antilog}[\log(\text{original value}) - \log(\text{estimated values})]$.

The original value was SR calculated for each tooth area. The estimated value is the SR estimated from a specific allometric formula formed by the macaques. If these two values were equal to each other, RD was equal to 1, meaning colobines express the same value as macaques. A larger or smaller value than the original one for the colobines (compared with macaques) was indicated by RDs that were larger or smaller than 1, respectively. One-way ANOVA was used to explore the differences of the residuals between the colobines and the macaques. The residuals were also used to compute the matrix of Euclidean Distances between each of the colobine genera and the macaque, allowing assessment of overall differences when all residuals were considered together.

Principal Components Analysis (PCA), to examine

whether or not there is any notable variation among the taxa, was used to further analyze the residuals. It answered the question: is there a marked separation among the Asian colobine genera while being examined against the macaques on the same continent?

2 Results

Allometric formulae of cranial length against SR of the teeth for Asian macaques are listed in Tab. 2. Each tooth shows a significant relationship with the cranial

Tab. 2 Allometric relationships between dental measurements and cranial length in macaques

	Upper teeth			Lower teeth		
	<i>r</i>	<i>a</i>	<i>b</i>	<i>r</i>	<i>a</i>	<i>b</i>
I1	0.540*	3.713	0.621	0.502*	3.941	0.563
I2	0.688**	3.565	0.793	0.673**	3.875	0.636
C	0.817**	3.958	0.442	0.795**	4.065	0.413
P3	0.733**	3.444	0.808	0.804**	3.914	0.494
P4	0.729**	3.344	0.844	0.776**	3.379	0.849
M1	0.715**	3.120	0.865	0.730**	3.171	0.886
M2	0.739**	3.143	0.796	0.738**	3.191	0.799
M3	0.761**	3.366	0.699	0.796**	3.252	0.729

The correlation between each dental variable and cranial length reaches significant levels at $P < 0.05$ (*) or at $P < 0.01$ (**).

Notes: *r*, correlation coefficient; *a*, constant; *b*, exponent.

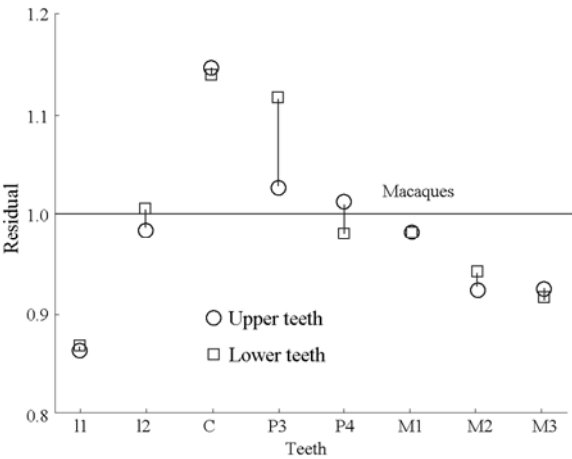


Fig. 1 Average dental residuals of the Asian colobines, referring to the allometric formulae of the macaques on the same continent

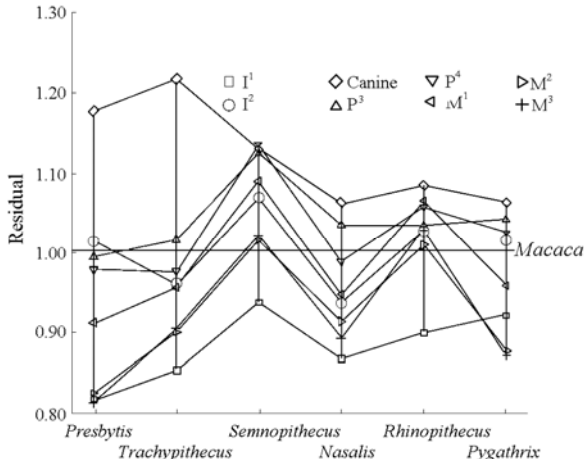


Fig. 2 Comparison of the dental residuals for the upper teeth among the genera of the Asian colobines, referring to the allometric formulae of the macaques on the same continent

length, judged by very high correlation coefficients. All teeth are, however, negatively scaled ($b < 1.00$) relative to the cranial length, particularly the incisors, canines and P3s.

Residuals for the Asian colobines, derived from the allometric formulae combining the macaques, are illustrated in Fig.1. Except for P3s, which show large residuals, the teeth display very similar residual patterns in each jaw. In comparison with macaques, colobines express smaller residuals for I1s and M1-3s but larger for canines and P3s. Residuals of the I2s and P4s are almost equal to those of the macaques.

Dental comparisons based on the residuals—between each genus of the Asian colobines and *Macaca*—are provided in Figs. 2 and 3. ANOVA results for the upper teeth indicate that, compared with macaques, *Presbytis* shows significantly larger canine, but smaller molar residuals; except for the two premolars, the teeth for *Trachypithecus* have significantly smaller residuals; *Semnopithecus* displays significantly larger I², premolars and M¹, but smaller I¹, residuals; the residuals for canine and P³ of the *Nasalis* are significantly larger, but those for the incisors and molars are significantly smaller; with regard to *Rhinopithecus*, the canine, P⁴ and M¹ have significantly larger, but I¹ displays significantly smaller, residuals; as for *Pygathrix*, the canine and P³ residuals are significantly larger but those for the other three teeth (I¹ and two molars - M¹ and M³) are significantly smaller.

A profile similar to that of the upper teeth exists in the lower teeth. Thus, the lower incisors, canines and P₃ for *Presbytis* are significantly larger, but I₁ and the three molars show significantly smaller residuals; canine and P₃ residuals of *Trachypithecus* are significantly larger, but those for I₁ and the last two molars are significantly smaller; the residuals of the canines and P₃, M₂ and M₃ in *Semnopithecus* are significantly larger and smaller than macaques, respectively; *Nasalis* shows significantly larger P₃, but significantly smaller canine and M₃ residuals; *Rhinopithecus* displays significantly larger M₁ and M₂, but significantly smaller canine residuals; three residuals for *Pygathrix*, namely I₂, canine and P₃, are significantly larger, but those for I₁ and three molars are significantly smaller.

Eigenvalues and eigenvectors for the first three axes of PCA based results of the residuals are listed in Tab. 3. More than seventy percent (73.69%) of the total variation is explained (45.44%, 15.14% and 13.11% being accounted for by each respective axis). The

eigenvectors for upper and lower teeth are very similar: the three molars, canines and P3s, and the incisors make large contributions to generic dispersion along the first three axes, respectively. P4s also show positive values (contributions) in the first axis.

A dispersal diagram of the 6 Asian colobine genera along the first three axes of PCA is shown in Fig. 4. There is a clear separation among them along the first axis; *Rhinopithecus* and *Semnopithecus* are more positively, while *Trachypithecus* and *Presbytis* are more negatively, allocated, and *Nasalis* and *Pygathrix* are in the middle of the axis. Despite their similarity, echoed by the first axis, the second axis markedly separates *Rhinopithecus* from *Semnopithecus*. The separation among the other genera along the same axis is less apparent. The third axis remarkably separates *Pygathrix* from *Presbytis*, but separation among others is less noticeable.

Euclidean Distances among the Asian colobines and macaques, based on residuals of all the teeth, are listed in Tab. 4. The distances between macaques and each of the colobine genera are illustrated in Fig. 5. A distance subsequences of the colobines from the macaques is thus formed: *Presbytis* > *Trachypithecus* > *Semnopithecus* > *Nasalis* > *Pygathrix* > *Rhinopithecus*.

Tab. 3 Eigenvectors of the first three axes of PCA based on dental residuals of Asian colobines

	Comonents		
	1	2	3
Total variation%	45.44	15.14	13.11
Cum. Variation%	45.44	60.58	73.69
Eigenvector			
Upper teeth			
I1	0.518	0.033	0.569
I2	0.393	0.177	0.606
C	-0.290	0.749	-0.174
P3	0.519	0.503	-0.294
P4	0.772	0.309	-0.096
M1	0.931	0.017	-0.106
M2	0.923	-0.083	-0.177
M3	0.855	-0.078	-0.226
Lower teeth			
I1	0.554	0.186	0.677
I2	0.269	0.304	0.755
C	-0.410	0.758	0.082
P3	-0.171	0.795	-0.239
P4	0.644	0.334	-0.130
M1	0.887	-0.016	-0.141
M2	0.946	-0.051	-0.114
M3	0.881	-0.146	-0.228

3 Discussion

The results obtained from dental morphometric variations in this study provide some interesting evidence in assessing the relationships both within Asian colobines and between the colobines and the macaques on the same continent.

A significant result was that dental variation depends upon different components of the dentition as explored by PCA. Thus, eigenvectors in Tab. 3 indicated that the upper and the lower teeth have very similar profiles. This should be expected given the two jaws work together as a masticatory unit. Some results in the study, however, show that different parts of the unit express alternative contributions to the variation analysis. Thus, molars dominate the dispersal (variation) patterns of the cercopithecoids along PC1. However, the contributions of I1s and P4s to PC1 cannot be ignored, though smaller than those of the molars; they show reasonably high positive eigenvectors; canines and premolars dominate PC2; and the incisors dominate PC3.

When teeth are considered individually, the findings

of Hylander (1975a, b), Kay (1975) and Kay & Hylander (1978) imply that colobines have smaller incisors and larger molars than macaques. They postulate that this combination of features may have been related to the increased use of the incisors in macaques for seizing and cutting fruits, and the increased use of the molars in colobines for the chewing, crushing and grinding of the strong fibers in leaves and grasses. The analyses here provided a different profile: only I1s show a smaller size in colobines than that in macaques, molars in the colobines, however, are of a larger size than those in the macaques. This may be due to the factors that different analytic methods were/are used – residuals were not used in those studies. The larger size of the molars for colobines found in this study, are confirmed by one investigation (Kay, 1978) in which only M2s were analysed.

Such inconsistencies may also be associated with the spectrum of the taxa used for different studies; the species used by Hylander (1975a, b), Kay (1975) and Kay & Hylander (1978) included the taxa on both continents. It is only when the Asian species alone are compared (as in this investigation) that the new finding is

Tab. 4 Euclidean Distances among the genera of the Asian cercopithecoids, based on allometric residuals

	<i>Presbytis</i>	<i>Trachypithecus</i>	<i>Semnopithecus</i>	<i>Nasalis</i>	<i>Rhinopithecus</i>	<i>Pygathrix</i>	<i>Macaca</i>
<i>Presbytis</i>	0.000	0.246	0.573	0.343	0.576	0.277	0.570
<i>Trachypithecus</i>	0.246	0.000	0.433	0.223	0.403	0.243	0.437
<i>Semnopithecus</i>	0.573	0.433	0.000	0.388	0.263	0.392	0.364
<i>Nasalis</i>	0.343	0.223	0.388	0.000	0.354	0.199	0.350
<i>Rhinopithecus</i>	0.576	0.403	0.263	0.354	0.000	0.363	0.213
<i>Pygathrix</i>	0.277	0.243	0.392	0.199	0.363	0.000	0.322
<i>Macaca</i>	0.570	0.437	0.364	0.350	0.213	0.322	0.000

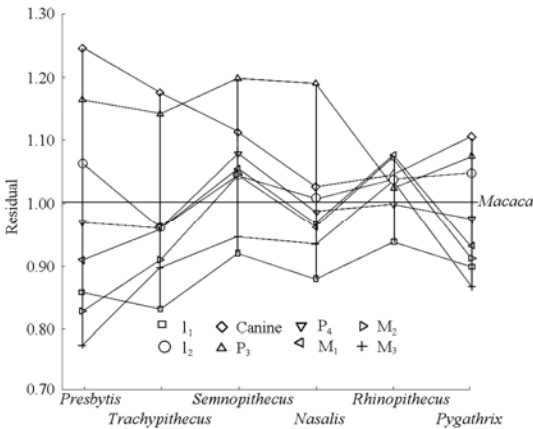


Fig. 3 Comparison of the dental residuals for the lower teeth among the genera of the Asian colobines, referring to the allometric formulae of the macaques on the same continent

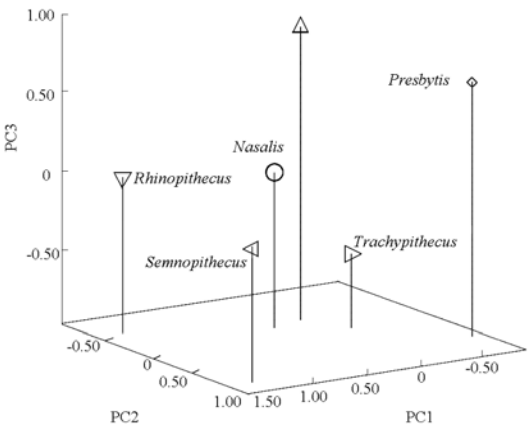


Fig. 4 Dispersal patterns of the Asian colobines along the first three axes of PCA, based on the residuals derived from the allometric formulae of the macaques on the same continent

evident. A comparison among the taxa within the same continent alone will reveal some issues associated with the shared macro-geographic and environmental changes. In other words, although the two groups of Asian Old World monkeys do indeed have different dietary preferences, the functional adaptations to those preferences may not be as great as previously assumed.

After separation from the hominoids in the Early Miocene (Fleagle, 1999; Stauffer, et al, 2001), the ancestors of the Asian colobines and macaques diverged one from another, and migrated at different times from Africa to Eurasia (Stewart & Disotell, 1998; Fleagle, 1999), following the expanding distribution of the hominoids in Eastern Asia by the latest Middle Miocene (Kunimatsu et al, 2004). Survivors of both groups, finally spread to Asia (Delson, 1994; Delson, et al, 2000). They then radiated out throughout Asia at about the same time, though the colobines may have arrived a little earlier than the macaques (Pan & Jablonski, 1987; Fa, 1989; Delson, 1994). Both groups have existed during the same series of tectonic and climatic changes in Asia since the Early Pleistocene, especially the rapid uplift of the Qinghai-Tibet Plateau and the last global glaciation. It is therefore possible that they evolved some common characteristics under the similar environmental and climatic conditions. This could mean that the two groups on the same continent have developed some similarities in relationships between teeth and body size, compared with the scenarios of which the taxa of the two continents are considered. In other words, some major differences in the last 5 million years between Africa and Asia, in terms of climate, geographical landscape and vegetation (Gollop & Foley, 2002), could have led to major functional differences in digestive systems, dietary preferences and tooth variation. Such differences may be less prominent between species on the same continent, as this study sought to analyse.

Differences among the genera of the Asian colobines show a great deal of variation when teeth are analyzed individually (Figs. 2 and 3) and together (Fig. 4). These included: 1) large molars – even larger than those found in the macaques – that characterize *Rhinopithecus* and *Semnopithecus* (Fig. 4): they are closely grouped and noticeably separated from the others along PC1; 2) a grouping comprising *Nasalis* and *Pygathrix* in the middle of PC1 (Fig. 4); 3) the two genera, *Pygathrix* and *Presbytis* that display a noticeable separation from the other genera along the third axis; and

4) generic separations along PC2 are generally indistinct, except for the propinquity of *Semnopithecus* to *Presbytis* and their combined separation from the odd-nosed species (*Rhinopithecus*, *Pygathrix* and *Nasalis*).

In general, the relationships among Asian colobines found in this study further emphasize the results reported in a previous investigation (Pan & Oxnard, 2003), in which only Asian colobines were analyzed. The differences in dental structure among the Asian colobines seem to reflect specific geographical and environmental adaptations. These include the limitation of *Rhinopithecus* to the Qinghai-Tibet Plateau and the Qingling Mountain – *R. bieti* inhabits areas up to 4,500 meters above sea level where no other non-human primate lives, with unique dietary adaptations to the special vegetation in this cold environment (Shi et al, 1982; Hu et al, 1989; Li & Shi, 1989; Liu, 1989; Bleisch et al, 1993; Bleisch & Xei, 1998; Kirkpatrick, 1998; Kirkpatrick et al, 2001). The grey langurs analyzed in these studies were collected from Punjab, Sikkim and Chambai in India, also the regions close to the Qinghai-Tibet Plateau. In contrast *Nasalis* and *Pygathrix* are normally distributed in tropical, moist, deciduous and semi-deciduous forests along the coastline (Lippold 1995, 1998; Bennett & Davies 1994) where they are known to feed on a very high proportion of leaves and seeds along coastal swamps and riversides (Banks, 1949; Davis, 1962; Kern, 1964). Thus, the relationships among Asian colobines, revealed by PCA, seem to reflect principally their similarities in geographic distribution and ecological adaptation.

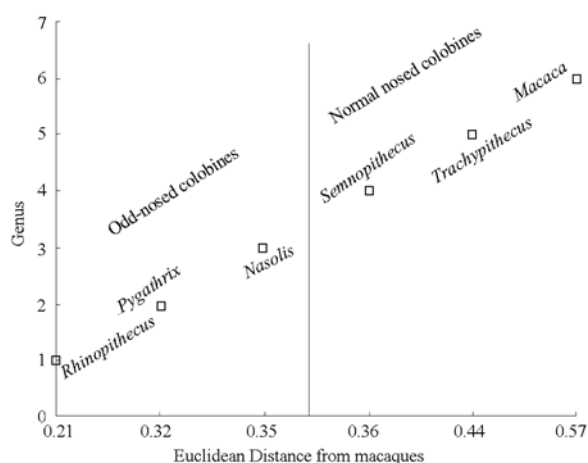


Fig. 5 Euclidean Distances of the Asian colobines, based on the residuals derived from the allometric formulae of the macaques on the same continent

The results relating to the grey langurs and the snub-nosed monkeys on PC2, reflected by specifically developed canines and premolars, could be due to the differences in social structure and behavior. However, such comparative information is not yet available.

Some other results, in particular the profiles illustrated in Fig. 4, may also reflect episodes related to the evolutionary differences among the Asian colobines. Thus, all the odd-nosed species are separated from the normal-nosed taxa (*Presbytis* and *Trachypithecus*) and are allocated on the positive side of PC1. *Semnopithecus* is the exception, but this species is significantly separated from *Rhinopithecus* and the other odd-nosed species along PC2, in which *Semnopithecus* is closely grouped with *Trachypithecus* and *Presbytis*. In other words, there is an obvious segregation between the odd-nosed and the normal-nosed Asian colobines referring to the profiles illustrated by the first two axes of PCA that account for most of the total variation (Tab. 3). This could be associated with the fact that these two colobine groups experienced quite different processes of evolution and radiation in Asia (Peng & Pan, 1994; Jablonski, 1998a,b).

Overall, the dental variations revealed by PCA imply that there exists a significant difference among the Asian colobines, which may be related to the variations in geographic diversity and phylogenetic development. In contrast, when Euclidean Distances between the colobines and the macaques were examined – in order to illustrate how far each of the Asian colobine genera is from the macaques – the profiles seemed to reflect phylogenetic relationships alone (Fig. 5). The profiles may also display divergence scenarios between the cercopithecines (to which the Asian macaques belong) and the Asian colobines; they have been postulated to have separated in the Miocene period (Pilbeam & Walker, 1968; Simons, 1969; Shoshani et al, 1996). Thus, colobines are now distinguished from macaques anatomically by the absence of cheek pouches, reduced thumbs and the presence of an elaborate sacculated stomach (Stewart & Disotell, 1998). The ancestor of the Asian colobines, *Mesopithecus*, is hypothesized to have followed a wooded savanna ‘corridor’ into Europe. Most of the European colobines demonstrated terrestrial or cursorial locomotion in their woodland, subtropical and temperate forest environments (Delson, 1994). The palaeoenvironment of *M. pentelicus* in Pikermi and other European areas in the later Miocene (Turolian) was

predominantly woodland, found throughout Eurasia (Leopold, 1969; Axelrod, 1975; Ioakim and Solounias, 1985), and there was a high degree of similarity to the present-day forests and woodlands of Kanha in India and a similarity to other Asian regions, especially in Sichuan (China). According to Jablonski (1998a, b), the ancestral stock of the odd-nosed langurs, most likely occupied the woodland (broadleaf deciduous) and subtropical woodland (broadleaf evergreen) habitats that were widely spread from western through to eastern Asia during the late Miocene and early Pliocene. These ecological niches were very similar to those which the modern odd-nosed colobines have adapted to in the East and parts of Southeast Asia. They include conifer forests (Solounias & Dawson-Saunders, 1988), the main environment for the Chinese snub-nosed monkeys in Sichuan (*R. roxellana*), the Qinghai-Tibet Plateau (*R. bieti*) and the Yuan-Gui Plateau (*R. brelichi*) adjacent to the Qinghai-Tibet Plateau (Pan & Oxnard, 2003). Further south, the odd-nosed colobines have diverged more and more from this habitat, from *R. avunculus* in Vietnam to those of Laos, Cambodia and Southeast Asia (Borneo and the Mentawais) – *Pygathrix*, *Nasalis* and *Simias* (Pan & Oxnard, 2001b). This implies that the diet of *Mesopithecus pentelicus* was very similar to those of the odd-nosed species – moister leaves, fruit and bark, fewer young leaves, leaf shoots and flowers, than with *Presbytis* and *Trachypithecus*. The two studies based on dental micro-wear also indicates a more frugivorous diet in *M. pentelicus* (Reitz & Benefit, 2001; Reitz, 2002).

Other reports indicate that *Mesopithecus pentelicus*, a well-represented Eurasian colobine fossil species, was more closely related to the odd-nosed species than to the other Asian colobines (Jablonski, 1998b; Groves, 2000; Pan et al, 2004).

The evidence gathered implies that the odd-nosed colobines are more closely related to ancestral Asian colobines that shared similarities with cercopithecines.

4 Conclusion

This study provides insight into understanding the issues associated with dental variation in Asian colobines, and a variation profile between the colobines and the macaques that settled down in Asia at different times. The following are the conclusions drawn:

When Asian colobines are regarded as a whole, and compared with more frugivorous Asian macaques, the

expectation of relative smaller front teeth is true only for IIs. Asian colobines also, unexpectedly, display relatively smaller molars. This may be related to the fact that all the Asian Old World monkeys have experienced similar environmental changes, due to tectonic movement and climate change in the last 5 million years. In other words, although African and Asian colobines and macaques show markedly different food preferences and dental morphological variation, the segregation between the two groups on Asia is less prominent.

Dental variation among the Asian colobine genera seems to be mainly due to the differences in their ecological niches. The snub-nosed monkeys and the grey langurs (*Rhinopithecus* and *Semnopithecus*) are quite different from other colobines, showing relatively larger molars than the macaques. This implies that they share similar ecological niches on the plateaus. Further studies on other anatomical parts, such as the maxilla and the mandible, are necessary to confirm this hypothesis.

Euclidean Distances between each of the Asian colobine genera and macaques illustrates their evolutionary development, mirroring the divergence between all colobines and cercopithecines. A further

study including African colobines is necessary to confirm such a postulation.

Acknowledgments: We are especially grateful to Dr. NG Jablonski, who provided some of the data collected from the American Museum of Natural History, New York; British Museum (Natural History), London; Field Museum of Natural History, Chicago; Museum National d'Histoire Naturelle in Paris; Natural Museum of Natural History, Washington, DC; and Royal Ontario Museum, Toronto. We would also especially like to thank Ms. Paula Jenkins and Mr. Richard Harbor for their help at the British Museum (Natural History), London. Our thanks also to Shanghai Natural History Museum, Shanghai; Nanchong Teachers College, Sichuan; East China Normal University, Wuhan; and Zoology Institute of Beijing for their enthusiastic help in data collection. We also thank the two anonymous reviewers who provided very valuable suggestions and comments on the manuscript. This work is supported by the National Research Foundation (NRF) and the Paleontology Scientific Trust (PAST), South Africa.

References:

- Andrews R, Harrison T, Delson E, Bernor RL, Martin L. 1996. Distribution and biochronology of European and Southwest Asian Miocene catarrhines. In: Bernor RL, Fahlbusch V, Mittmann, HW, editors. The evolution of western Eurasian Neogene mammal faunas[M]. New York: Columbia University Press, 168-207.
- Axelrod D. 1975. Evolution and biogeography of the Madrean Tethyan sclerophyll vegetation[J]. *Ann Mo Bot Gard*, **62**: 280-334.
- Banks E. 1949. Bornean mammals[M]. Kuching: The Kuching Press.
- Bennet EL, Davies AG. 1994. The ecology of Asian colobines. In: Davies AG, Oates JF, editors[M]. Colobine monkeys: their ecology, behavior, and evolution, 129-172. Cambridge: Cambridge Univ. Press.
- Bleisch W, Cheng AS, Ren XD, Xie JH. 1993. Preliminary results from a field study of wild Guizhou snub-nosed monkeys (*Rhinopithecus brelichi*)[J]. *Folia Primatol*, **60**: 72-82.
- Bleisch WV, JH Xie. 1998. Ecology and behavior of the Guizhou Snub-nosed langur (*Rhinopithecus* [Rhinopithecus] *brelichi*), with a discussion of the socioecology in the genus. In: Jablonski NG, editor. The natural history of the doucs and snub-nosed monkeys[M]. Singapore: World Scientific, 217-239.
- Bouvier M. 1986. Biomechanical scaling of mandibular dimensions in New World monkeys[J]. *Int J Primatol*, **7**: 551-567.
- Brandon-Jones D. 1998. Pre-glacial Bornean primate impoverishment and Wallace's line. In: Hall R, Holloway JD, editors. Biogeography and geological evolution of SE Asia[M]. Leiden, the Netherlands: Backbuys Publisher, 393-404.
- Caton J. 1998. The morphology of the gastrointestinal tract of *Pygathrix nemaeus* (Linnaeus, 1771). In: Jablonski NG, editor. The natural history of the doucs and snub-nosed monkeys[M]. Singapore: World Scientific, 129-152.
- Chapman CA, Chapman LJ, Gillespie TR. 2002. Scale issues in the study of primates foraging: red colobus of Kibale National Park[J]. *Am. J. Phys. Anthropol*, **117**: 349-363.
- Davies AG, Oates JF. 1994. Colobine monkeys: their ecology, behavior and evolution[M]. Cambridge: Cambridge University Press.
- Davis DD. 1962. Mammals of the lowland rainforest of north Borneo[J]. *Bulletin National Museum Singapore*, **31**: 1-129.
- de Winter W. 1997. Perspectives on mammalian brain evolution: Theoretical and morphometric aspects of a controversial issue in current evolutionary thought. PhD thesis[M]. Western Australia: University of Western Australia.
- Delson E, Terranova CJ, Jungers WL, Sargis EJ, Jablonski NG. 2000. Body mass in Cercopithecidae (primates, mammals): estimation and scaling in extinct and extant taxa[J]. *Anthropological Papers of the American Museum of Natural History*, **83**: 1-159.
- Delson E. 1980. Fossil macaques, phylogenetic relationships and a scenario of development. In: Lindburg DF, editor. The macaques: studies in ecology, behaviour and evolution[M]. New York: Van Nostrand Reinhold, 10-30.
- Delson E. 1994. Evolutionary history of the colobine monkeys in paleoenvironmental perspective. In: Davies AG, Oates JF, editors.

- Colobine monkeys: their ecology, behavior and evolution[M]. Cambridge: Cambridge University Press, 11-43.
- Disotell TR. 1996. The phylogeny of Old World monkeys[J]. *Evol Anthropol*, **5**: 8-24.
- Eaglen RH. 1984. Incisor size and diet revisited: the view from a platyrrhine perspective[J]. *Am J Phys Anthropol*, **64**: 263-275.
- Fa JE. 1989. The genus *Macaca*: a review of taxonomy and evolution[J]. *Mammal Rev*, **19**: 45-81.
- Fleagle JG. 1999. Primate adaptation and evolution, 2nd ed[M]. San Diego: Academy Press.
- Fooden JG. 1982. Ecogeographic segregation of macaque species[J]. *Primates*, **6**: 574-579.
- Freedman L. 1957. The fossil Cercopithecoidea of South Africa[J]. *Ann Transvaal Mus*, **23**: 121-257.
- Gingerich PD, Smith BH, Rosenberg K. 1982. Allometric scaling in the dentition of primates and predictions of body weight from tooth size in fossils[J]. *Am J Phys Anthropol*, **58**: 81-100.
- Goldstein S, Post D, Melnick D. 1978. An analysis of cercopithecoid odontometrics. I. The scaling of the maxillary dentition[J]. *Am J Phys Anthropol*, **49**: 517-532.
- Gollop PJ, Foley RA. 2000. Evolutionary geography, habitat availability and species distributions among early African hominids. In: Harcourt CS, Sherwood BR. editors[M]. *New Perspectives in Primate Evolution and Behavior*. Smith Settle Limited. Otely, West Yorkshire LS21, 29-46.
- Gordon KD. 1982. A study of microwear on chimpanzee molars: implication for dental microwear analysis[J]. *Am J Phys Anthropol*, **59**: 195-215.
- Gould SJ. 1975. On the scaling of tooth size in mammals[J]. *Am Zool*, **15**: 351-362.
- Groves CP. 2000. The phylogeny of the Cercopithecoidea. In: Whitehead PF, Jolly CJ. editors. *Old World monkeys*[M]. Cambridge: Cambridge University Press, 77-98.
- Hanya G. 2004. Seasonal variations in the activity budget of Japanese macaques in the coniferous forest of Yakushima: effects of food and temperature[J]. *Am J Primatol*, **63**(3): 165-77.
- Hanya G, Noma N, Agetsuma N. 2003. Altitudinal and seasonal variations in the diet of Japanese macaques in Yakushima[J]. *Primates*, **44**(1): 51-9.
- Hu JC, Den QX, Yu ZW. 1989. A study of the ecological biology of the golden monkey. In: Chen FG, editor. *Progress in the studies of golden monkey*[M]. Xian, China: Northwestern University, 208-215.
- Hylander W. 1975a. Incisor size and diet in *Cercopithecoidea*[J]. *Am J Phys Anthropol*, **42**: 309.
- Hylander W. 1975b. Incisor size and diet in anthropoids with special reference to *Cercopithecidae*[J]. *Science*, **189**: 1095-1098.
- Ioakim C, Solounias N. 1985. A radiometrically dated pollen flora from the upper Miocene of Samos Island, Greece[J]. *Rev Micropaléontol*, **28**: 197-204.
- Jablonski NG, Whitfort MJ, Roberts-Smith Nola, Qinqi X. 2000. The influence of life history and diet on the distribution of catarrhine primates during the Pleistocene in eastern Asia[J]. *J Hum Evol*, **39**: 131-157.
- Jablonski NG. 1998a. The evolution of the douc and snub-nosed monkeys and the question of the phyletic unity of the odd-nosed colobines. In: Jablonski, NG, editor. *The natural history of the doucs and snub-nosed monkeys*[M]. Singapore: World Scientific, 13-53.
- Jablonski NG. 1998b. The response of catarrhine primates to pleistocene environmental fluctuations in East Asia[J]. *Primates*, **39**: 29-37.
- Jungers WL. 1985. Body size and scaling of limb proportions in primates. In: Jungers, WL, editor. *Size and scaling in primate biology*[M]. New York, Plenum Press, 345-381.
- Jungers WL, Burr DB, Cole MS. 1998. Body size and scaling of long bone geometry, bone strength and positional behaviour in cercopithecoid primates. In: Strasser E, Fleagle JG, Rosenberger AL and McHenry HM, editors[M]. *Primate locomotion: recent advances*, New York, Plenum Press, 309-331.
- Kay R, Hylander WL. 1978. The dental structure of mammalian folivores with special reference to primates and phalangerioidea (Marsupialia). In: Montgomery GG. editor. *The ecology of arboreal folivores*[M]. The National Zoological Park: Smithsonian Institution, 173-191.
- Kay RF. 1975. The functional adaptations of primate molar teeth[J]. *Am J Phys Anthropol*, **43**: 195-216.
- Kay RF. 1978. Molar size and diet in extant Cercopithecidae. In: Butter PM, Joysey KA, editor. *Development, function and evolution of teeth*[M]. New York: Academic Press, 309-339.
- Kay RNB, Davies AG. 1994. Digestive physiology. In: Davies AD, Oates JF, editors. *Colobines monkeys: their behavior, ecology and evolution*[M]. Cambridge: Cambridge University Press, 299-249.
- Kern JA. 1964. Observation on the habits of the proboscis monkey, *Nasalis larvatus* (Wurmb.), made in the Bruei Bay area. Borneo[J]. *Zoologia*, **49**: 183-192.
- Kieser JA, Groeneveld HT. 1990. Static intraspecific allometry of the dentition in *Otolemur crassicaudatus*[J]. *Zool J Linnean Soc*, **98**: 295-306.
- Kirkpatrick RC, Zou RJ, Zhou HW. 2001. Digestion of selected foods by Yunnan snub-nosed monkey *Rhinopithecus bieti* (Colobinae)[J]. *Am J Phys Anthropol*, **114**: 156-162.
- Kirkpatrick RC. 1998. Ecology and behavior in snub-nosed and douc langurs. In: Jablonski, NG, editor. *The natural history of the doucs and snub-nosed monkeys*[M]. Singapore: World Scientific, 115-190.
- Kunimatsu Y, Ratanasthien B, Nakaya H, Saegusa H, Nagaoka S. 2004. Earliest Miocene hominoids from Southeast Asia[J]. *Am J Phys Anthropol*, **124**: 99-108.
- Leopold E. 1969. Late Cenozoic palynology. In: Tschudy RD, Scoot RA, editor. *Aspects of palynology*[M]. New York: Wiley Interscience, 377-438.
- Li GH, Shi CD. 1989. Food of the golden monkey. In: Chen FG, editor. *Progress in the studies of golden monkey*[M]. Xian, China: Northwestern University, 222-224.
- Lippold, LK. 1995. Distribution and conservation status of douc langur in Vietnam[J]. *Asian Primates*, **4**: 4-6.
- Lippold LK. 1998. Natural history of douc langurs. In: Jablonski, NG, editor. *The natural history of the doucs and snub-nosed monkeys*[M]. Singapore: World Scientific, 191-206.
- Liu SF. 1989. A preliminary investigation of the golden monkey in Qing-Ling Mountains. In: Chen FG, editor. *Progress in the studies of golden monkey*[M]. Xian, China: Northwestern University, 201-206.
- Napier JR, Napier PH. 1967. *A Handbook of Living Primates*[M]. London: Academic Press.
- Oates JF, Davies AG, Delson E. 1994. The diversity of living colobines. In: Davies AG, Oates JF, editors. *Colobine monkeys: their ecology, behavior and evolution*[M]. Cambridge: Cambridge University Press, 46-73.
- Pan RL, Oxnard CE, Groves C. 2004. Relationships between the fossil Colobine *Mesopithecus pentelicus* and extant Cercopithecoids, based on Dental Metrics[J]. *Am J Primatology*, **62**: 287-299.

- Pan RL, Oxnard CE, Milne N. 2002. Mandibular variation among Chinese macaques[J]. *Am J Primatol*, **56**: 99-115.
- Pan RL, Oxnard CE. 2001a. A metrical dental analysis of the golden monkey (*Rhinopithecus roxellana*)[J]. *Primates*, **42**: 23-33.
- Pan RL, Oxnard CE. 2001b. Cranial Morphology of the Golden Monkey *Rhinopithecus* and Douc Langur (*Pygathrix nemaeus*)[J]. *Hum Evol*, **6**: 199-223.
- Pan RL, Oxnard CE. 2003. Phylogenetic Similarities or Functional Adaptations? Dental Variation Among Asian Colobine Monkeys[J]. *Zool. Studies*, **4**(1): 93-105.
- Pan RL, Peng YZ, Ye ZZ, Wang H, Yu FH. 1992. Classification and relationship of the Macaque population on Hainan Island, China[J]. *Folia Primatol*, **59**: 39-43.
- Pan RL, Peng YZ. 1995. Body size of *Macaca anderssoni* and its offspring[J]. *Hum Evol*, **10**: 283-287.
- Pan RL. 1998. A Craniofacial Study of The Genus *Macaca*, with special Reference to the Stump-tailed Macaques, *M. arctoides* and *M. thibetana*: A Functional Approach[M]. PhD Thesis, The University of Western Australia, Australia.
- Pan YR, Jablonski NG. 1987. The age and geographical distribution of fossil cercopithecids in China[J]. *Hum Evol*, **2**: 59-69.
- Peng YZ, Pan RL. 1994. Systematic classification of Asia Colobines[J]. *Hum Evol*, **9**: 25-33.
- Pilbeam D, Grould SJ. 1974. Size and scaling in human evolution[J]. *Science*, **186**: 892-901.
- Pilbeam D, Walker A. 1968. Fossil monkeys from the Miocene of Napak, northeast Uganda[J]. *Nature*, **220**: 657-660.
- Pirie PL. 1978. Allometric scaling in the postcanine dentition with reference to primate diets[J]. *Primates*, **19**: 583-591.
- Reitz J, Benefit BR. 2001. Dental microwear in *Mesopithecus pentelici* from the late Miocene of Pikermi, Greece[J]. *Am J Phys Anthropol*, **114** (Sup): 125.
- Reitz J. 2002. Dietary adaptation of late Miocene Colobinae[J]. *Am J Phys Anthropol*, **117**(Sup): 129-130.
- Rowe N. 1996. The pictorial guide to the living primates[M]. East Hampton and New York: Posonias Press.
- Shi DC, Li GH, Fu TL. 1982. Preliminary ecological research in golden monkeys[J]. *Zool Res*, **3**: 105-110.
- Shoshani J, Groves CP, Simons EL, Gunnell F. 1996. Primate phylogeny: Morphological vs molecular results[J]. *Molecular Phylogeny and Evolution*, **5**: 102-154.
- Simons EL. 1969. Miocene monkey (*Prohylobates*) from northern Egypt[J]. *Nature*, **223**: 687-689.
- Smith R J, Jungers WL. 1997. Body mass in comparative primatology[J]. *J H Evol*, **32**: 523-559.
- Smith RJ, Petersen CE, Gipe DP. 1983. Size and shape of the mandibular condyle in primates[J]. *J Morphol*, **177**: 59-68.
- Smith RJ. 1983. The mandibular corpus of female primate taxonomic, dietary, and allometric correlates of interspecific variation in size and shape[J]. *Am J Phys Anthropol*, **61**: 315-330.
- Solounias N, Dawson-Saunders B. 1988. Dietary adaptations and paleoecology of the late Miocene ruminants from Pikermi and Samos in Greece[J]. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **65**: 149-172.
- Stauffer RL, Walker A, Ryder OA, Lyons-Weiler M, Hedges SB. 2001. Human and ape molecular clocks and constraints on Paleontological hypotheses[J]. *The American Genetic Association*, **92**: 469-474.
- Stewart CB, Disotell TR. 1998. Primate evolution -in and out of Africa[J]. *Current Biology*, **8**: R582-588.
- Willis MS, Swindler DR. 2004. Molar size and shape variations among Asian colobines[J]. *Am J Phys Anthropol*, **125**: 51-60.
- Wood BA. 1979. An analysis of tooth and body size relationships in five primate taxa[J]. *Folia Primatologica*, **31**: 187-211.
- Ye ZZ, Peng YZ, Liu RL, Zhang YP. 1987. The gross anatomy of the golden monkeys[M]. Kunming, China: Yunnan People's Publication House.
- Yim WS, He XX. 1988. Holocene formaminifera in Hong Kong and their Palaeoenvironmental significance. In: White P, Aigner JS, Jablonski NG, Taylor G, Walker D, Wang PX, editors[M]. (eds.): The palaeoenvironment of east Asian from the Mid-Tertiary. Vol. 2. Hong Kong: Centre of Asia Studies, 787-809.
- Zhao QK, Deng ZY, Xu JM. 1991. Natural foods and their ecological implications for *Macaca thibetana* at Mount Emei, China[J]. *Folia Primatol*, **57**(1):1-15.

本刊主编张亚平院士当选为 TWAS 院士

在 2007 年 11 月 13—14 日发展中国家科学院 (TWAS, 原名为第三世界科学院) 举行的第 18 届全体院士大会上, 昆明动物研究所所长、本刊主编张亚平院士荣誉当选为 TWAS 院士。

TWAS 院士是从发展中国家的科学院、国家研究理事会、大学和研究机构的著名科学家中选举产生的。在本次 TWAS 大会上, 有 45 名科学家当选为 TWAS 院士, 张亚平院士是我国当选的 7 名院士之一。

11 月 19 日, 发展中国家科学院副院长、中国科学院常务副院长白春礼发来贺信, 代表中国科学院并以其个人名义对张亚平院士荣誉当选致以衷心的祝贺和崇高的敬意。